

Seagrass Primary Production — a Review*

R. J. WEST and A. W. D. LARKUM

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Seagrasses dominate many inshore benthic communities in Australia and contribute a high proportion of the total fixed carbon of the inshore ecosystem. The methods in use to measure primary production of seagrass communities with special reference to Australia are reviewed, and some of the comparable results listed. Seagrass productivity is a reflection of climate, local environmental conditions, and individual growth strategies of particular species, but is high in comparison with most other plant communities.

Light, temperature, salinity, nutrients, sediment and human influence are reviewed as possible controls on seagrass production.

R. J. West, N.S.W. State Fisheries, P.O. Box N211, Grosvenor Street, Sydney, Australia 2001, and A. W. D. Larkum, School of Biological Sciences, University of Sydney, Sydney, Australia 2006; manuscript received 19 May 1981, accepted for publication in revised form 16 December 1981.

INTRODUCTION

Production refers to the capacity of a biological system to form organic matter, and the rate of this formation is called productivity. Primary production is the capture of radiant solar energy by plants and subsequent conversion of carbon and water to organic matter during photosynthesis.

The measurement of primary productivity is of importance as it can give an indication of the capability of a biological system to support a food web of secondary producers and leads to a better understanding of the growth strategies of plant species.

Productivity measurements have the units dry matter produced per unit area per unit time, usually expressed as grams dry weight per square metre per day, or tonnes dry weight per hectare per year. When the relationship between carbon content and dry weight of the plant material is known, then another useful unit is grams carbon per square metre per hour. Although dry weight has been used extensively in this review, one should bear in mind that the variability in ash content (interspecific, and seasonal) may make comparisons of productivity in terms of dry weight misleading. Wherever necessary, the values of McRoy and McMillan (1977) have been adopted for the sake of comparison. These authors report that 'available data on eelgrass indicate an organic weight of about 80% of the dry weight, 47% of which is carbon'.

There are two broad methods often used to measure primary productivity (Larkum, 1981). One is based on the calculation of net photosynthetic rates, while the other is a measure of growth. The former is a short-term method, the period of experimentation being from a matter of minutes, to perhaps as long as twenty-four hours, and involves the measurement of radioactive carbon fixation or of net oxygen production. The latter is a long term method, based on the increases in the dry matter over a period of weeks, months or years.

In most seagrasses, at least three processes, photorespiration (Larkum, 1981), the loss of dissolved organic carbon (Brylinsky, 1977) and formation and translocation of carbon reserves (Dawes and Lawrence, 1979), will ensure that net photosynthesis and growth are not equivalent over the short term. Despite this, direct comparisons of the methods have been attempted (Bittaker and Iverson, 1976).

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METHODS OF MEASUREMENT

The short-term methods of estimation of primary production include measurement of oxygen production, or of radioactive carbon uptake (Vollenweider, 1971). Both of these methods may be affected by the recycling of gases in the extensive lacunal system possessed by most seagrasses (Zieman, 1968; McRoy and McMillan, 1977).

Methods employed to measure oxygen release from seagrass communities may involve the use of closed vessels, such as glass bottles or large acrylic chambers, or they may involve measurement in open waters (Vollenweider, 1971). The principal method of oxygen determination is the Winkler chemical method (Strickland and Parsons, 1972), although oxygen electrode techniques are also widely in use (Pijanowski, 1975).

Diurnal oxygen concentrations in a flowing water mass provided one of the earliest short term measures of productivity of aquatic plants (Odum, 1956, 1957). This method made no allowances for planktonic metabolism, and relied heavily on a crude estimate of water volume and speed. Loss of oxygen through bubbling, and changes in concentration due to reaeration were further problems. Several later studies relied on this method (Odum, Burkholder and Rivero, 1959; Quasim and Bhattathiri, 1971). Improvements have been made to this technique by the measurement of the planktonic contribution (through the use of light and dark bottles), and of the oxygen reaeration (Nixon and Oviatt, 1972). A further improvement is in the isolation of a known volume of water (Weiner and Kirkman, 1980).

A variation of the above technique is the collection of whole plants (or of leaf sections) which are subsequently incubated in glass jars either *in situ* or under controlled laboratory conditions, and assayed for oxygen production (Jones, 1968; Buesa, 1974; Drew, 1978).

The most sophisticated method employed in the measurement of oxygen release from seagrass communities is the simultaneous recording of oxygen, temperature, light and salinity within a completely enclosed chamber, with circulating seawater (Weiner and Kirkman, 1980; Clough and Attiwill, 1980). Clough and Attiwill (1980) have used this method to predict the primary productivity of *Zostera muelleri* in Western Port Bay, Victoria. These authors have calculated a photosynthetic response curve from several diurnal incubations. This treatment could be substantially improved by increasing the number of diurnal incubations to exclude seasonal variations in photosynthesis, and by the continuous measurement of light at the plant-canopy level. However the problem created by the existence of internal gas lacunae remains unresolved.

Wetzel (1964) and Drew and Larkum (1967) pioneered the *in situ* use of radioactive isotopes to measure primary productivity of aquatic plants. These workers used bell jars to incubate single plants which were later assayed for carbon-14. McRoy (1974) adopted a similar method with the seagrass *Zostera marina* in Alaskan waters, while Drew and Jupp (1976) measured uptake by *Posidonia oceanica* in Mediterranean waters. Penhale (1977) measured primary productivity of *Thalassia testudinum* and its epiphytes by a carbon-14 method, this time improved by the reduction of unstirred layers through the circulation of the seawater surrounding the plants. The use of radioisotopes in the field is somewhat difficult and does not overcome the problem of the possible recycling of gases in the lacunae (McRoy and McMillan, 1977).

Long term methods of measurement of primary productivity were first used in relation to seagrasses in Denmark in the early part of this century. Petersen (1913) estimated the primary productivity of *Zostera marina* by harvesting this seagrass at several stages of its growth cycle, and concluded that these plants made an important contribution to production in the estuarine system. He did not however take into account the rapid turnover of leaf material that is often characteristic of seagrasses, for

example, of many *Zostera* species (Sand-Jensen, 1975). Petersen's estimates were therefore very much lower than the true production rates. Such biomass figures are still often used as an estimate of productivity of plants (Westlake, 1963), although turnover of biomass is the more important concept. This can be defined as the number of times mean biomass is replaced throughout the annual growing cycle:

$$\text{Turnover} \quad = \quad \frac{\text{Annual increase in biomass}}{\text{mean biomass}}$$

(crops per year)

Zieman (1968, 1974, 1975) developed a marking technique to measure leaf production in meadows of *Thalassia testudinum* in waters off Florida. This method was described at the International Seagrass Workshop in the Netherlands as the only reliable method to measure directly leaf production of seagrasses (McMillan *et al.*, 1973). It has been used in many studies involving *Thalassia testudinum* (Zieman, 1975; Patriquin, 1973; Greenway, 1977), *Zostera marina* (Sand-Jensen, 1975) and *Posidonia australis* (West and Larkum, 1979; Kirkman and Reid, 1979).

Few workers have attempted to measure rhizome growth in seagrasses. Patriquin (1973) introduced a method based on the time interval between new leaf production, the dry weight of rhizome sections, and the number of leaf scars on the rhizome. This method appears to work adequately for *Thalassia testudinum* and *Posidonia australis* (West, 1980). Sand-Jensen (1975) has used the increase in shoot numbers in fixed quadrats to estimate rhizome production for *Zostera marina*.

COMPARISON OF PRODUCTIVITY MEASUREMENTS

The results of many productivity studies have been summarized elsewhere (McRoy and McMillan, 1977; Zieman and Wetzel, 1980). These authors have made little or no reference to the many different methods adopted in the individual productivity studies. However, in this review, the recommendation of the International Seagrass Workshop held in the Netherlands (McMillan *et al.*, 1973) is adopted, and only results based on leaf-making techniques are included.

Some representative values for leaf-production of several seagrass species are shown in Table 1, and some available data concerning rhizome production shown in Table 2.

There are often large differences in biomass between stands of the same seagrass species, depending on localized environmental conditions, and this leads to variations in the productivity estimates between such stands. The differences in biomass may be due to different shoot densities, or variability in leaf length and width. West and Larkum (1980) compared five study sites and found large variations in biomass, densities and leaf characteristics between stands of *Posidonia australis*, however leaf turnover was relatively constant (2.8–4.5 crops of leaves per year). This consistency in mean leaf turnover is also apparent from a number of studies carried out on various seagrass species (Table 1), although seasonal variations often mask the observation. Thus it would seem that for many seagrass species, the number of leaves produced each year by individual shoots may be quite consistent, although biomass, density and leaf characteristics vary, depending on local conditions, such as depth, sediment, age of bed, degree of wave exposure and exposure to salinity changes.

Thus care must be taken when assessing the productivity of a large area. It is not often possible to make an estimate of the area of seagrass beds, as say by aerial photography and then to multiply this area by the productivity found for plants in an experimental area. Plant density is not always linearly related to plant cover (Larkum *et al.*, in press) and plant cover is what is usually estimated from aerial photography.

TABLE 1
Estimates of Seagrass Leaf-production

Seagrass	Locality	Climate	Biomass g.dw/m ²	Productivity g.dw./m ² /day	Turnover	Reference
<i>Thalassia testudinum</i>	Florida Jamaica Bermuda	tropical tropical tropical	280 (mean) 249 (mean)	2.2-10.0 6.0 (mean) 1.2-14.8	2.9-13 8.7 (mean) 1.2-14.8	Zieman, 1975 Greenway, 1976 Patriquin, 1973
<i>Posidonia australis</i>	N.S.W. N.S.W. W.A.	warm-temperate warm-temperate warm-temperate	300-500 400. 400	1.0-5.5 2.5 5.3	2.8-4.5 2.3 (mean) 4.3 (mean)	West & Larkum, 1979 Kirkman & Reid, 1979 Cambridge, 1979
<i>Posidonia sinuosa</i>	W.A.	warm-temperate	660	3.9	2.1 (mean)	Cambridge, 1979
<i>Zostera capricorni</i>	N.S.W. N.S.W.	warm-temperate warm-temperate	55 26	3.6 0.5	24.0 (mean) 7.0 (mean)	McComb <i>et al.</i> , 1981 Larkum (unpub)
<i>Heterozostera tasmanica</i> *	Victoria	cold-temperate	27-173	0.34-4.2	1.5-7.2	Bulthuis, 1981
<i>Zostera marina</i>	Denmark	cold-temperate	443	7.9	6.5 (mean)	Sand-jensen, 1975

* Standing crop — includes leaf and erect stem.

TABLE 2
Estimates of Seagrass Rhizome Production

Seagrass	Locality	Climate	Biomass g.d.w./m ²	Productivity g.d.w./m ² /day	Turnover Crops/Yr.	Reference
<i>Thalassia testudinum</i>	Bermuda	tropical	—	4.4	—	Patriquin, 1973
<i>Posidonia australis</i>	N.S.W.	temperate	> 1000	0.15 (mean)	< 0.05	West, 1980
<i>Zostera marina</i>	Denmark		—	1.5 (mean)	—	Sand-Jensen, 1975

Larkum *et al.* (in press) found that a detailed analysis of the beds of *Zostera capricorni* in Botany Bay gave a productivity value which was 5 fold lower than the estimate obtained by the simple product of total area and a productivity value obtained in a dense, shallow bed.

From the data available (Table 2) it would appear that rhizome production is extremely variable between species. Rhizome production is obviously a reflection of the growth habit of individual species, and the stability of a particular seagrass stand. For example, West (1980) has shown that turnover of rhizome material is slow, but depends markedly on site, in stands of *Posidonia australis* in Botany Bay. Some erect shoots may be more than 20 years in age (cf Kuo and Cambridge, 1978). Other seagrasses must exhibit a high turnover of rhizomes, as these species appear to replace rhizome annually (personal observation).

In general, it may be said that the production of organic matter in seagrass beds occurs at a high rate when compared with most other plant communities (Westlake, 1963), and is a reflection of climate, local environmental conditions and individual growth strategies of particular species.

CONTROLS ON PRODUCTIVITY

Although turnover of organic matter may be consistent in established stands of seagrasses, there are many factors which can influence the biomass that can be achieved or which influence the seasonality in growth at particular sites, and some of these factors will now be discussed.

Light and temperature

Light is the most critical ecological factor for plant growth as it directly affects the rate of photosynthesis. The lower depth limit to the establishment of seagrasses is generally considered to be due to the minimum light intensity required by a particular seagrass (Phillips, 1978), although few conclusive experiments have been performed. Ostensfeld (1905) was one of the first workers to attempt to correlate distribution patterns of a seagrass (*Zostera marina*) to underwater irradiance.

The short term methods of measuring productivity (see earlier) generally yield information concerning the effect of light on photosynthetic rate, however the variability in methods and light units measured makes comparison of this work difficult. For example, Jones (1968) and Buesa (1974, 1975) have used leaf sections isolated in bottles, Drew (1978) used leaf slices in small jars, McRoy (1974) used whole plants in jars, Penhale (1977) used whole plants in circulating seawater, and Clough and Attiwill (1979) used whole plants (*in situ*) in benthic chambers. Most of these workers used different measures of light intensity.

Drew (1979) has compared the photosynthetic response of six seagrass species, and found that, in all cases, a classic P-I curve for plants intermediate between sun and shade adaptation could be demonstrated and that thermal damage occurred above 30-35°C. Further this author has found that at least one species, *Halophila stipulacea*, is capable of a chloroplast re-orientation that may be a protective mechanism in high light situations. Trocine, Rice and Wells (1981) have also noted chloroplast clumping in a *Halophila* species and suggest that this results in an increased photosynthetic tolerance to ultraviolet-B radiation.

McRoy and McWilliam (1977) suggest that production can be expressed in terms of light quantity. They report three separate studies giving estimates of between 5.3-117.0 microgram carbon per langley per gram biomass, and propose that the similarity in result may lead to a useful relationship from which productivity could be estimated from light intensity.

Backman and Barilotti (1976) have shown that turion density of *Zostera marina* is reduced when irradiance is reduced. Thus these authors present perhaps the best evidence to show that a coastal development that affects turbidity will also affect seagrass growth and production.

Temperature is also known to affect photosynthetic rates of seagrasses (Biebl and McRoy, 1971), and the effect of high temperature on the growth of some species is well documented (Zieman, 1975; Thorhaug, Blake and Schroeder, 1978). Zieman (1975) found that leaf production in *Thalassia testudinum* was near zero at temperatures above 35°C or below 25°C.

The interaction of light and temperature in field situations makes the individual effects of these environmental variables difficult to study, and has led to some disagreement and confusion as to whether light, or temperature, is responsible for seasonality of growth rates of seagrasses. The variation in method for the measurement of seagrass production (i.e. leaf growth or photosynthetic rate) also adds to the confusion. From our own studies with *Posidonia australis* it would appear that temperature controls individual leaf growth rates provided that light intensity has remained sufficiently high to allow the plants to accumulate reserves in the rhizome (West, 1980; West and Larkum, in preparation).

Salinity

There are few references in the literature to the effect of salinity changes on seagrass productivity. Biebl and McRoy (1971) report a reduction in photosynthesis, when salinity is reduced from seawater, for *Zostera marina*, while Ogata and Matsui (1965) found for *Zostera nana* that a reduction in photosynthesis with increasing salinity above seawater was due principally to carbon limitation.

Other laboratory studies have involved the transplantation of seagrasses to aquaria at various salinities (McMillan and Mosely, 1967; McMahan, 1968; McMillan, 1974). McRoy and McMillan (1977) summarize these results: '*Halodule* shows that broadest salinity tolerance . . . *Halophila* the narrowest . . . and *Thalassia* and *Syringodium* show intermediate tolerance'.

Zieman (1975) found that productivity decreased above and below the optimum salinity of 30 parts per thousand for *Thalassia testudinum*.

West (1980) found that large short term changes in salinity could cause mortality of *Posidonia australis*, but there was no significant effect on leaf growth of surviving plants.

The effect of salinity on establishment of seagrass species requires further studies so that an attempt to explain distribution patterns can be made.

Sediment and nutrients

Little is known concerning the sediment requirements of most seagrasses although some general observations have been listed by Den Hartog (1970). For example, *Posidonia australis* generally occurs on sandy substratum, whereas *Zostera capricorni* is not restricted to sand, and grows on a wide range of substrates (Harris, King and Ellis, 1979).

One advantage that seagrasses have over most algae is that they are not dependent on the nutrient availability in the water column. Both anatomical studies and physiological experiments indicate that seagrasses can take advantage of the often rich nutrient supply offered by the sediment and interstitial water.

Kuo and Cambridge (1978) found a reduced vascular system in *Posidonia australis*, but all the elements required for nutrient uptake and transfer were present. Further, McComb *et al.* (1981) suggest that the wide occurrence of bacterial colonies, fungi and

other micro-organisms found in the rhizosphere and peripheral root tissue of *Posidonia australis* may be involved in nutrient uptake and nitrogen fixation in seagrass roots. Further evidence exists for the occurrence of nitrogen fixation in either the phyllosphere or rhizosphere of other seagrasses (Patriquin and Knowles, 1972; Goering and Parker, 1972). Capone *et al.* (1979) have found a relationship between productivity (biomass) and nitrogen fixation in the *Thalassia testudinum* community.

McRoy, Blackburn and Klug (1981) have suggested that the level of nitrogen fixation and sulphur reduction in sediments associated with seagrasses is related to the successional stage of the seagrass community.

Phosphate absorption has been demonstrated for the roots and rhizomes of eelgrass (McRoy and Barsdate, 1970; Penhale and Thayer, 1980), and for *Posidonia australis* (Larkum, unpublished data).

Human influence

The effect of man on seagrass productivity is a result of industrial and urban development along shallow marine embayments and along coastal fringes. Thayer, Wolfe and Williams (1976) have summarized many of the impacts of man on seagrass systems. Light, salinity, water turbulence and nutrient levels are all affected by the degree of foreshore development, and toxic contamination, dredging and 'filling-in' should be added as further possible impacts.

Evidence exists for a decline in *Posidonia australis* beds near urban areas in New South Wales, South Australia and Western Australia (Larkum, 1977). There has been a continued reduction in the area colonized by *Posidonia australis* in Botany Bay (N.S.W.) through both increased turbidity and water turbulence (Larkum, 1976; West, 1980). Aerial photographic evidence confirms the loss of 20% in the area covered by seagrasses, in Botany Bay, in the last fifteen to twenty years. A decline of *Posidonia australis* in Cockburn Sound, Western Australia, has also been described (Cambridge, 1975, 1979). Similar situations have been documented for the meadows of *Posidonia oceanica* off the French coastline (Meinesz and Laurent, 1978).

The recovery of seagrass communities in degraded areas may be extremely slow, even if the environmental stress is relieved. This results from the fact that many seagrasses appear to rely heavily on vegetative reproduction, and rhizome growth is often very slow. Artificial revegetation is difficult and costly and thus careful management of existing seagrass areas is imperative.

SECONDARY PRODUCTION

As stated, seagrasses produce large quantities of organic matter. Seagrass meadows also offer a diverse habitat for secondary producers (Kikuchi and Peres, 1977).

Although leaf material may be grazed quite heavily in tropical areas by fish (Ogden, 1976), turtles (Hirth, Klikoff and Harper, 1973) and dugongs (Heinsohn, Wake, Marsh and Spain, 1977) there are few direct grazers in temperate regions (Kikuchi and Peres, 1977). Conacher *et al.* (1979) have shown that the major fish grazer of *Posidonia australis*, *Monacanthus chinensis* removes less than 1% of the productive capacity. Nevertheless these fish do obtain some nutrients from ingested leaf fragments. Kirkman and Reid (1979) have studied the role of a seagrass (*P. australis*) in the carbon-budget of an estuary. Only 3% of the total seagrass biomass (in terms of carbon) was consumed by herbivores, whereas the remainder was lost as exuded dissolved organic carbon and detached leaves in approximately equal proportions.

Thus, secondary production in temperate regions occurs primarily through the detrital food chain (Fenchel, 1977):—

1. Leaching of dissolved organic and inorganic materials,
2. Mechanical breakdown of leaves (waves or ingestion),
3. Bacterial and fungal decomposition,
4. Attack by bacteriovorous microfauna and detritivores,
5. These small fauna are prey for large carnivores.

GENERAL CONCLUSIONS

Care is required in the selection of a method to measure productivity and Zieman's leaf marking technique (Zieman, 1974) is still preferred.

Primary production of many seagrass species is high and related to growth strategy of individual species and local environmental conditions.

The ability of seagrasses to inhabit sandy substrates, to use sediment nutrients, and to accumulate carbon reserves are important factors which ensure a relatively stable food supply and habitat, and this is reflected in a diverse and important faunal community.

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